TRICHILOGASTER MAIDENI (FROGGATT) (HYMENOPT., CHALCIDOIDEA), A WASP CAUSING GALLS ON *ACACIA IMPLEXA* BENTH., AND *A. MAIDENI* F.v.M.

WITH OBSERVATIONS ON AUSTRALIAN CHALCIDOID GALLS.

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(Plate viii; five Text-figures.)

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Introduction.

From 1935 to the close of 1938 the writer had under observation galls formed on the petioles and stems of Hickory (*Acacia implexa*)† growing in the Sydney district. These were mainly at the junction of the petiole of the phyllode, and incorporated some of the latter, and occasionally portion of the stem as well. The galls, which reached maturity in the late spring, were then rather irregular in shape, dark brown, rough-surfaced and woody (Pl. viii, C).

A. implexa, which suckers freely, grows very abundantly in the northern suburbs of Sydney, and the majority of the trees examined were galled. The height of the galled trees ranged from only eighteen inches up to ten feet. On the smaller trees the galls were scattered along the main stem, but in larger trees they were mainly on the laterals.

Emergence of wasps from these galls extended over a period of many months during the late spring, and then on through the summer and autumn, and even into the following winter. In the spring of 1936 just prior to the emergence of any adults, large numbers of galls were placed in containers, and the insects emerging were found to include twelve species of Hymenoptera, of which nine were Chalcidoids. These latter included *Trichilogaster maideni* (Froggatt), and when subsequently females of this species were enclosed with young new growth of *A. implexa* which was abundant on the trees at the time, they readily oviposited therein. The trees which were two years old were isolated, and growing at the home of the writer. In the following spring a limited number of the typical galls developed. All the other species of Chalcidoids were at various times enclosed with such young growth on *A. implexa*, but displayed no interest.

In the present paper the life-history of this species of gall-forming *Trichilogaster* is set out, together with notes on some of the other species of gall inhabitants. The writer (1940) discussed the life-history of *Trichilogaster acaciae-longifoliae* (Froggatt), a perilampid wasp causing galling of the flower buds of *Acacia* spp., in the Sydney district, and pointed out that there is difficulty in distinguishing, on a morphological basis, various described species in the genus *Trichilogaster*.

From 1935 to 1937 the writer also made observations on elongate fleshy galls on the stems of *Acacia Maideni* (Pl. viii, D). These were seen only on two trees, one at Roseville and the other at Artarmon, suburbs of Sydney, and were far less common than the galls on *A. implexa*. A species of *Trichilogaster* was bred from these galls, and

* This is the last of a series of papers on Australian Chalcidoidea, submitted in August, 1937, to the University of Sydney, in fulfilment of the requirements for the degree of Doctor of Science in Agriculture. Some observations made after that date are also included.

† The writer wishes to acknowledge his indebtedness to Mr. R. H. Anderson, National Herbarium, Sydney, for his identifications of the various species of *Acacia* mentioned.

though slightly different in size and colour, was identical morphologically with *Trichilogaster maideni* bred from the galls on *A. implexa*. As will be pointed out later when discussing this species in relation to the galls on *A. Maideni*, there are a number of points in its biology and in its host associations in which it differs constantly from *Trichilogaster maideni* on *A. implexa*. While no attempt will be made to designate subspecific or varietal names for the two forms under discussion, the ways in which théy differ from one another and also from Froggatt's specimens of *Trichilogaster maideni*, will be set out, and it is felt that when more detailed taxonomic studies of the genus as a whole are undertaken, it will be desirable to give subspecific or varietal names to the various forms at present considered as *Trichilogaster maideni*.

In their morphology and biology the forms of *Trichilogaster maideni* causing galls on *A. implexa* and on *A. Maideni*, resemble very closely *Trichilogaster acaciae-longifoliae* (Froggatt) (see Noble, 1940).

TRICHILOGASTER MAIDENI CAUSING GALLS ON ACACIA IMPLEXA.

MORPHOLOGY.

The Adult.

Froggatt (1892) described this species as *Cynips maideni*, stating that the specimens were bred from thick fleshy galls on the twigs of *Acacia longifolia* at Elizabeth Bay and Rose Bay, Sydney. Referring to Froggatt's description, Girault (1916) stated: "Froggatt does not describe the species *maideni*. This is such a case of carelessness as to cause astonishment. His pseudo-description represents nothing like the actual specimens." Mayr (1905) established the genus *Trichilogaster* and redescribed *Trichilogaster* (*Cynips*) *maideni*, this being the type species of the genus. The writer examined specimens of *T. maideni* bred by Froggatt from one of the type localities, and apart from some colour variation, these differed little from specimens bred by the writer from *A. implexa*.

The female of *Trichilogaster maideni* (Fig. 1) from *Acacia implexa* averages 2·95 mm. in length, and has the head, thorax and abdomen mainly black, apart from

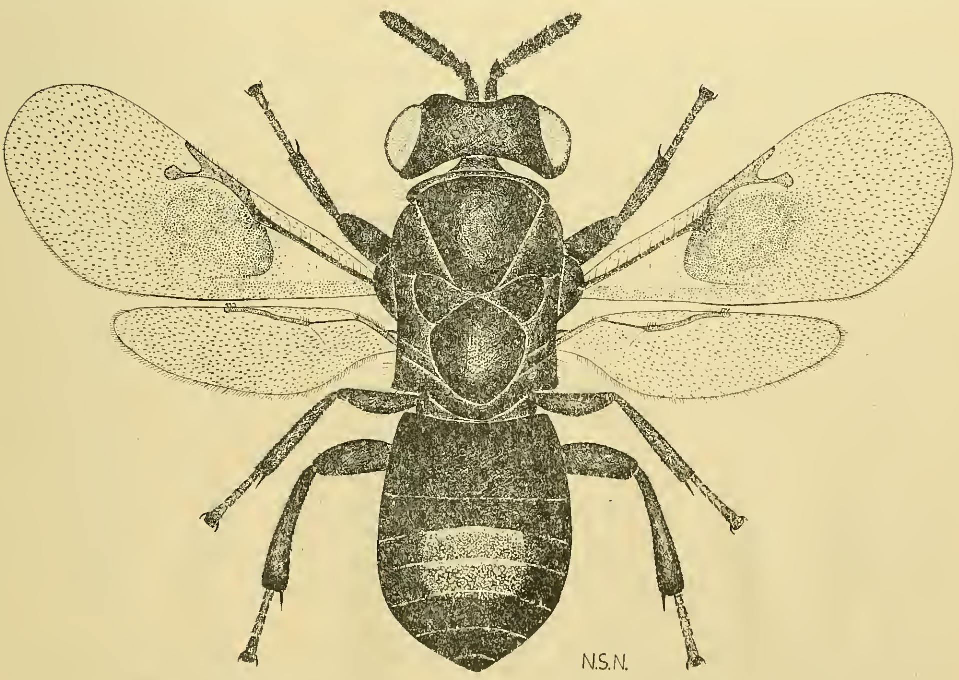

Fig. 1.—*Trichilogaster maideni* (Froggatt). Adult female from galls on *Acacia implexa* (× 22).

a variable ochreous patch on the dorsal surface of the third and fourth abdominal segments. This light patch stands out quite clearly in specimens preserved in alcohol, but in dry mounts the abdomen contracts and this light patch is mainly hidden, the abdomen then appearing entirely black. The eyes are red, the antennae are brown to dark brown; the venation is brown, the submarginal vein being a darker shade than the remainder. The coxae, trochanters and all but the distal portions of the femora are dark brown to black. The remainder of the legs are brown to ochreous, there being some variation in different individuals. The surface of the thorax is shining and rugose, the corrugations running in wavy transverse lines. There is a fuscous patch on each forewing, a notable feature being the scant development of the setae on the wings. The setae are particularly short and are sparsely scattered, and are wanting from their upper margins.

In different individuals there is some variation in the depth of pigmentation of the various parts. In some the dorsal surface of the first and second abdominal segments is only dark brown, and in others there is a narrow ochreous patch on the front margin of the fifth abdominal segment, while in others the third segment is dark brown and only very little lighter than either the first or second. In general appearance the female is rather robust, being broad in proportion to its width, and the abdomen is slightly depressed.

The antenna (Fig. 2E), the mandible (Fig. 2F), the stigmal knob (Fig. 2G), the tip of the stylet (Fig. 2H) and the tip of the sheath of the ovipositor (Fig. 2I) are illustrated. It will be seen that neither the stylet nor the sheath is barbed, but the stylet is particularly sharp and curved.

Specimens of females of *Trichilogaster maideni* collected by Froggatt are much the same size as those bred by the writer from *A. implexa*. However, in Froggatt's mounted specimens examined by the writer the entire dorsal surface, except the first two segments and the tip, is ochreous. Moreover, there is an ochreous patch between the eyes and the lateral ocelli on the vertex and extending a variable distance down the face. The pronotum is ochreous, as also are the lateral margins of the scutum.

The Egg.

As with other primary gall wasps studied, the newly emerged female has the abdomen filled with fully developed eggs. Newly deposited eggs for study were obtained by placing females in tubes with uninfested Hickory twigs, the eggs being dissected out from the latter soon after deposition.

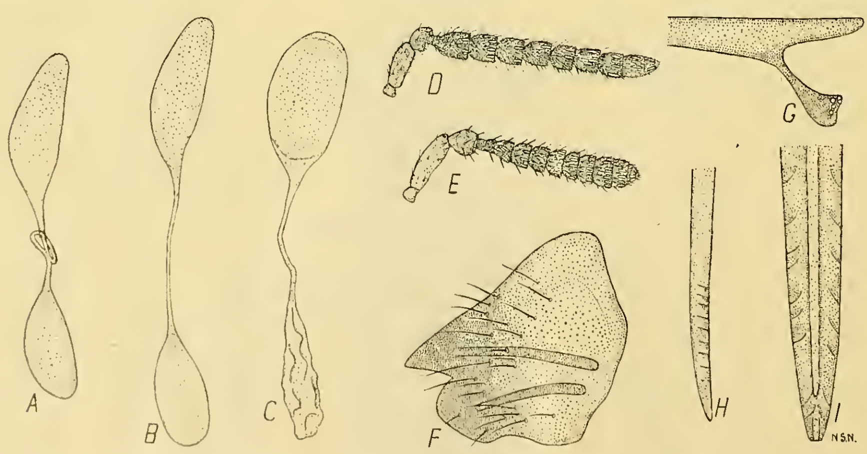

Fig. 2.—*Trichilogaster maideni.* A, B, Ovarian eggs (× 115); C, Egg twenty-four hours after deposition (× 115); D, Antenna of male (× 40); E, Antenna of female (× 40); F, Mandible of female (× 115); G, Stigmal knob of female (× 61); H, Lateral view of tip of ovipositor stylet (× 200); I, Ventral view of tip of ovipositor sheath (× 200).

The eggs are white, and in the ovary. consist of two large bodies joined by a narrow connecting tube which is at first folded (Fig. 2A), but just prior to deposition becomes extended (Fig. 2B) and after deposition all the protoplasm passes into one end of the egg, producing one white oval body, with a long twisted and flaccid pedicel (Fig. 2C). The dimensions of the egg are set out in Table 1. It will be seen that there is considerable variation in the dimensions of its two bodies, as well as in the total lengths of ovarian eggs with the connecting tubes extended. The average dimensions of the egg are remarkably similar to those of *Tepperella trilineata* (Noble, 1938*b*).

TABLE 1.

Dimensions of Egg of Trichilogaster maideni (*in Millimetres*).

	Mature eggs dissected from ovaries.							Eggs immediately after deposition.	
	Length with connecting tube folded.	Length with connecting tube extended.	Larger body.		Smaller body		Width of connecting tube.	Body length.	Body width.
			Length.	Width.	Length.	Width.			
Average ..	0·396	0·497	0·183	0·062	0·129	0·058	0·004	0·172	0·083
Maximum ..	0·409	0·538	0·198	0·066	0·139	0·069	0·005	—	—
Minimum ..	0·373	0·436	0·172	0·056	0·119	0·053	0·003	—	—

The Larva.

Based on the distribution and size of the integumentary setae, the shape and size of the mandibles, and the number and size of the spiracles, five larval stages can be recognized. The various larval stages of *T. maideni* in general appearance, in the distribution of setae and sensillae, and in the development of the respiratory system, are similar to the various larval stages of *T. a.-longifoliae*, details of which have already been published by the writer (Noble, 1940).

Stage I.—The mandible of the first stage larva (Fig. 3C) is very pale amber, and measures 0·007 mm. in length. The average width between the two anterior tentorial rami is 0·043 mm. The first stage larva is only just visible to the unaided eye, and the smallest larva measured was 0·18 mm. in length and 0·082 mm. in width.

Stage II.—The smallest second stage larva measured was 0·24 mm. in length and 0·16 mm. in width. The mandible which is amber, averages 0·015 mm. in length. The width between the two anterior tentorial rami is 0·096 mm., which is more than twice as wide as in the first stage.

Stage III.—The mandible of the third stage (Fig. 3D) is amber and averages 0·025 mm. in length. The smallest third stage larva measured was 0·46 mm. in length and 0·28 mm. in width.

Stage IV.—The fourth stage larva (Fig. 3A) resembles the fifth in many respects. The smallest larva measured was 0·74 mm. in length and 0·35 mm. in width. The mandible (Fig. 3E), which is light brown, is more heavily chitinized than in the preceding stages, but is still unevenly bidentate with one rather long curved tooth. It averages 0·036 mm. in length and is more or less triangular in outline. Occasionally, there is evidence of a division of the minute second tooth.

The larva, which is cylindrical and arched and tapering to both ends, consists of a head and thirteen segments, and is greenish-white. The distribution of setae and sensillae on the head is similar to that of the fifth stage. On the underside of the head, and dorsally and laterally on the first segment, and in very limited numbers on the dorsal surface of the second and third segment, are minute papillae, visible only at high magnifications. The abdominal segments carry setae of variable length and number, in different individuals. These are quite prominent on the first segment and form a complete median circlet. The length of these setae on the first segment varies on the same larva, the average length of the largest on a number of larvae measured, being 0·023 mm. On the second segment, the setae are much smaller, more limited in number and confined to the dorsal and lateral surface. On the succeeding segments, the distribution of these setae is variable. There is at least a pair of lateral setae on each segment and in some of the posterior segments the number varies from two to four. On the median segments these setae are only just visible at very high magnifications, but are slightly larger on the posterior segments.

The respiratory system is very well developed, there being nine pairs of spiracles, one pair on each segment from the second to the tenth inclusive. The first pair of spiracles is much the largest, and the third pair much the smallest. Internally, profusely branching tracheae pass to the various organs.

Stage V.—The fifth or last stage larva (Fig. 3B) which is white, is cylindrical and arched, and tapers conspicuously to both ends. It consists of a head and thirteen segments, segmentation being very distinct. The average length at maturity is 3·59 mm., the maximum being 3·75 mm. and the minimum 3·23 mm. The average width at the widest point is 1·23 mm., the maximum being 1·41 mm. and the minimum 0·83 mm. The mandible (Fig. 3F) is brown and bidentate, there being one large curved and sharp tooth, so that the general triangular outline is still maintained; its length averages 0·066 mm.

All over the first and second segments, and dorsally and laterally on succeeding segments, there are numbers of short pointed papillae, which become less numerous, smaller in size, and more confined to the dorsal surface on the posterior segments. In some larvae a very limited number of minute papillae are present on the ventral surface of the head. To the sides and also just above the mandibles, there is a pair of setae, and immediately beneath the mandibles there are two minute setae, three sensillae, and outside these two truncate cone-shaped structures of unknown function, and outside these and slightly below, there is a further pair of large setae.

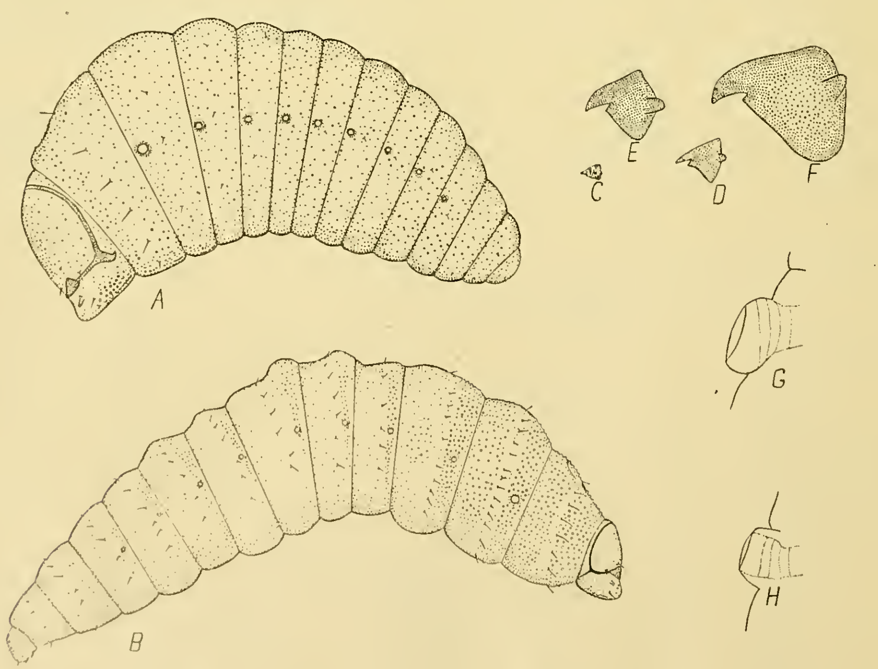

Fig. 3.—*Trichilogaster maideni.* A, Lateral view of fourth stage larva (× 78); B, Lateral view of mature larva (× 23); C, Mandible of first stage larva (× 256); D, Mandible of third stage larva (× 256); E, Mandible of fourth stage larva (× 256); F, Mandible of fifth stage larva (× 256); G, Lateral view of spiracle from second segment of mature larva (× 256); H, Lateral view of spiracle from third segment of mature larva (× 256).

Every segment of the body carries a large number of amber setae, which are quite long and stand out conspicuously. These setae vary greatly in size, even on the same segment, and in different larvae, some setae on the first segment being over three times the length of the smallest seta on the same segment. On all but the last segment these setae are in a fairy regular median circlet, and they completely surround the first three segments, being dorsal and lateral in all but the last segment, where prominent setae of variable size are scattered over the whole surface.

The respiratory system is very much the same as that of the preceding stage, nine pairs of open spiracles being present, and these project slightly from the general surface of the integument (Figs. 3G, H). The first pair of spiracles are the largest, and the third pair are slightly smaller than the remainder.

BIOLOGY.

The Adult.

As only limited numbers of adults of *T. maideni* emerged even though many hundreds of galls were collected, detailed longevity tests were not carried out. When kept in tubes with green twigs taken from Hickory trees and fed on honey and water, females lived only a few days.

Females are rather sluggish and can be handled with ease in the laboratory, and seldom take to flight. In the field on bright sunny days, however, they have been observed in flight, and they fly readily from tree to tree, but sustained flight was never observed.

Oviposition.

Just prior to the emergence of adults in the late spring, the host trees produce considerable quantities of new and delicate spring growth, there being on the ends of each branch, numbers of minute developing stems and miniature phyllodes.

Wasps are ready to lay immediately after emerging from the galls. A female, when about to oviposit, alights on a twig, and then crawls quickly up towards its tip until it encounters the new growth, and utilizing the tips of the antennae it finally selects a suitable oviposition site, which is usually at the point of union of the young phyllode and the stem. Occasionally, the egg is deposited within the base of the phyllode and less commonly directly in the stem, usually somewhere near its junction with the phyllode. In the process of oviposition, there is nothing unusual. The ovipositor is brought down independently, so that its tip rests on the plant surface, and it is then slowly worked down into the tissues. After depositing an egg, the ovipositor is withdrawn, the female moves slightly forward, and repeats the process a number of times in the vicinity of each phyllode.

Total Eggs Within Females.

In 1936 ten newly emerged females were found to contain the following eggs: 269, 369, 288, 346, 334, 343, 310, 388, 174 and 305, the average being 312·6. In October, 1937, the eggs in each of ten newly emerged females were found to range from 246 to 496, the average being 347·1, a figure which is somewhat higher than that obtained in the preceding spring.

Larval Development.

Five larval stages occur and have been described.

In 1936 adults of *T. maideni* were observed to emerge from 3rd November to 28th November, and as they oviposit immediately on emerging and the length of adult life is short, the greatest oviposition that year occurred during November.

In Table 2 are set out the results of the dissection of galls from 14th January to 20th September, 1937, the date on which the first adults were cut from the galls. In the spring of 1937, adults commenced emerging on 5th October, almost a month earlier than in the preceding year. It is evident that there is considerable variation in the time spent in the various larval stages, and that as early as 26th January, 1937, all larval stages were present, though it was not until 6th May, 1937, that fifth stage larvae were again dissected. It will be seen that the larval stage extended over a period of at least nine months, being far the longest period of the life-cycle, and that pupation occurred mainly in the early spring in September and October, there being some variation from year to year.

TABLE 2.
Results of Dissection of Galls on Acacia implexa *showing Stages of* Trichilogaster maideni *Present.*

Date of dissection.	No. of Cells examined.	Larvae. Stage I.	Stage II.	Stage III.	Stage IV.	Stage V.	Pupae.	Adults.
14.i.1937	2	—	—	1	1	—	—	—
26.i.1937	8	1	1	2	3	1	—	—
20.ii.1937	4	3	1	—	—	—	—	—
12.iii.1937	6	1	5	—	—	—	—	—
22 iv.1937	19	—	13	5	1	—	—	—
6.v.1937	10	—	—	—	8	2	—	—
25.vi.1937	32	—	—	1	9	22	—	—
22.vii.1937	24	—	—	—	—	24	—	—
12.viii.1937	33	—	—	—	2	31	—	—
31.viii.1937	24	—	—	—	—	24	—	—
20.ix.1937	59	—	—	—	—	8	50	1

First adult of *T. maideni* emerged 5.x.1937.
Last ,, ,, ,, ,, ,, 4.xi.1937.

The Pupa.

The pupa is at first white, but changes within a few days to dark brown to shining black. The average length of the female pupa is 2·67 mm., the maximum being 3·07 mm. and the minimum 2·19 mm. Odd pupae were cut from the galls during the latter half of September, 1936, and larvae were pupating freely during October.

Emergence of Adults.

In 1936, pupae of *T. maideni* were cut from galls and placed in petri dishes in the laboratory, and the first adult emerged on 21st October, thirteen days before the first adult ate its way out of the galls. Adults were found in the galls for the first time on 24th October, ten days before any emerged naturally. Emergence commenced on 3rd November, and continued until 28th November, 1936, a period of 26 days. In the spring of 1937, a much larger series of galls was collected from various localities in the northern suburbs of Sydney, and from these 343 adults of *T. maideni* emerged, the first emergence occurring on 5th October, and the last on 4th November. The emergence period varies somewhat from year to year, but emergence of adults takes place in the spring in October or November.

Time Spent in the Various Stages of the Life-Cycle.

The life-cycle is annual. Oviposition occurs mainly during October or November, and dissections early in January, 1937, showed that in all the cells examined larvae were present. As the pupal period is at most six weeks, it is evident that, as with the other gall species studied, the larval period is very extensive and occupies from nine to ten months.

OBSERVATIONS ON THE DEVELOPMENT OF THE GALLS.

The eggs are deposited at the junction of young phyllodes and stems, and oviposition occurs mainly during November.

Examination of the trees on 5th January, 1937, failed to reveal any unevenness in the petioles or stems, and first stage larvae were present at that time.

On 14th January, examination revealed very slight unevenness and swelling at the bases of some phyllodes, and on cutting these open both first and second stage larvae of *T. maideni* were found. It is therefore evident that as with other gall species, there is no external evidence of gall formation until some time after the larvae have hatched.

By 22nd January, 1937, minute but very definite swellings were visible. Some of these were entirely on the petioles of the phyllodes, others appeared to have formed partly on the young stem and partly on the phyllode, so that if the phyllode were torn off the fracture occurred through the middle of the gall. Less commonly the galls were to be seen developing in the stems themselves, between adjoining phyllodes.

A further examination on 18th February showed that the more advanced galls were now well developed, and up to a quarter of an inch in diameter, but on the petioles of many phyllodes swellings were only just commencing. These galls were almost all bright green both internally and externally.

Frequent observations were then made on subsequent gall development until the emergence of the adult wasps.

By the end of May, 1937, the galls (Pl. viii, A) were about half grown, and while all the galls were still quite easy to cut, and contained masses of cells containing a high percentage of fluid, the outer surface of many galls was cracked and rough, this imparting a dark grey colour to the galls. Other galls were still bright green and smooth-surfaced.

There was a steady increase in the size of the galls during July and August, and some appeared to have reached their full size at the close of the latter month, and the remainder of the galls reached their full size during September, when the gall-forming larvae within them had also reached maturity.

As the galls increase in size more and more of the green coloration is lost, and the gall surfaces become roughened, cracked and irregular with a layer of scaly bark through which a little green sometimes shows, though many galls still present an entirely brown appearance (Pl. viii, C).

The phyllode above the gall may persist at the time the galls mature, but as early as 21st July, 1937, a number of the phyllodes had died and dropped, leaving only the gall attached to the stem, while in other cases the phyllode, though dead, still persisted.

Throughout larval development the galls can be cut readily with a razor, and internally consist of green cells of high fluid content. With the continued growth of the galls and their contained larvae there is a steady decrease in the amount of moisture present. By the time the galls mature in September, though still cutting readily, they are very much drier and harder internally, and are becoming woody. At the time the adults are commencing to emerge, the galls are rough and irregular in shape, the surface being covered with dark brown to black scaly bark, and they are so hard and woody that they can only with difficulty be cut. On some of the smoother galls a reddish or maroon coloration is visible.

During the early larval stages, the plant tissues are in contact with the larvae, there being a well developed and extensive nutritive layer. Gradually the latter is consumed by the larvae and the galls become more and more woody; a considerable space develops round the larvae, and by the time they reach maturity the larvae are to be found in a cell which is many times their own volume. Compared with many other galls on acacias, these galls are comparatively small considering the number of occupants. The number in each of 127 galls ranged from 1 to 16, the average being 3·99 cells per gall, and galls containing ten or more cells were quite common. The partitions of plant tissue separating the larvae become smaller and smaller as the larvae feed, and at maturity they are only separated from one another by very narrow partitions.

Where there is no crowding the individual cells are oval or spherical, but where oviposition has been heavy, they may assume a great variety of shapes. Unilocular galls, which are not common, are at maturity more or less spherical, fairly smooth, and tinted with red or maroon on one side.

While in some areas the individual galls remain more or less distinct, in others, due to heavy oviposition in stems as well as petioles, rather long irregular galls develop, which incorporate a number of adjoining petioles and the intervening stem.

Though at maturity, the phyllodes above many galls have died and fallen, sometimes they may still be present and alive at the time the galls mature. Heavily galled lateral twigs frequently die soon after the adults have emerged, but less heavily infested twigs are less affected and have been seen carrying numbers of vacated galls, and apparently functioning normally, at least two years after the occupants have left. In other instances, the remains of vacated galls, many years old, have been seen scattered along limbs which are now quite large, alive and apparently normal.

INSECTS ASSOCIATED WITH T. MAIDENI IN GALLS ON ACACIA IMPLEXA.

Two species of Lepidoptera, one species of Coleoptera and twelve species of Hymenoptera were bred from the galls, but many of these occurred in limited numbers only.

It was found that a high percentage of the galls was mined by two species of moth larvae, and in many instances only the outer gall-covering remained. These larvae in mining thus destroyed the normal hymenopterous occupants of the galls, it being quite common to find in such mined galls, dead and mouldy larvae and pupae of *T. maideni* and other species. In galls collected and held in jars in the laboratory in the spring, the larvae on maturing left the galls and spun cocoons and pupated at the sides of the containers and between adjacent galls. Large numbers of adult moths emerged in October and November, 1936, and again in 1937.

A number of adults of the dried apple beetle, *Doticus pestilens*, emerged from the galls in November, 1936. The larvae of this Anthribid are known to develop in apples which have dried up on the trees, and it has been bred from woody excrescences on *Acacia decurrens* (Allen *et al.*, 1898).

The Hymenoptera included two species of Ichneumonid, one Braconid and nine Chalcidoids. One species of Ichneumonid belonged to the genus *Mesostenoideus*, while the other, which was more abundant, was *Poecilocryptus nigromaculatus* Cameron. This species has frequently been bred from galls in New South Wales. Pupae were found in the galleries mined by the lepidopterous larvae, this Ichneumon apparently being a parasite of these gall-miners. Adults of *P. nigromaculatus* emerged from 22nd October to 12th November, 1936.

The Chalcidoids bred included the primary gall former, *T. maideni*, *Coelocyba nigrocincta* Ash., three species of *Eurytoma*, including *Eurytoma gahani* Noble, *Eurytoma* sp. B., and two species of *Megastigmus* including *Epimegastigmus* (*Megastigmus*) *trisulcus*.

Epimegastigmus (Megastigmus) trisulcus.

This species has already been discussed by the writer (Noble, 1938*a*), having been bred from citrus stem galls, where it was found in cells together with the remains of the larvae of the primary gall former *Eurytoma fellis*.

Adults of this species emerged both before, during and after all of the adults of *T. maideni* had emerged from the galls on *Acacia implexa*. Moreover, adults of *E. trisulcus* continued to emerge periodically until 31st August, 1937, from galls which were mature, and were collected and placed in jars in October, 1936, and which during all this time (approximately ten months) were hard, dry and woody.

On 5th October, 1938, when examining some mature galls caused by *T. maideni* on *Acacia implexa*, an adult of *E. trisulcus*, which has a relatively long ovipositor, was observed with this organ completely embedded in the hard gall. A few minutes later this female removed the ovipositor, and after moving further along the surface of the gall and after playing the tips of the antennae over its surface, again oviposited. The gall was then removed and cut open, and in two cells within the gall, newly deposited eggs of *E. trisulcus* were found. In the first gall cell examined, the egg was adhering to a fourth stage larva of *Eurytoma* sp., the only living occupant of the gall cell, the host larva (*T. maideni*) on reaching the last larval stage having been killed. In the second cell the egg of *E. trisulcus* was adhering to the body of a mature larva of *Eurytoma* sp. which had completely devoured the host.

The newly laid egg of *E. trisulcus* is comparatively large (Fig. 4D) and is visible to the unaided eye as a white, glistening, smooth, oval body. Under the microscope it is seen to consist, in addition to the main body, of an anterior short pointed pedicel and a long posterior pedicel. The latter was twisted and flaccid, but measured approximately one and a half times the length of the body of the egg. The body of the egg was 0·416 mm. in length and 0·136 mm. in width. As these eggs were laid in mature galls, which would shortly be hard and dry, it would appear that the main source of food of the larva of *E. trisulcus* must be the other insect occupant of the gall. *E. trisulcus* occurring in galls on citrus, has been found in cells with only the remains of the host larva, and it is not known whether in the ovipositions observed, the larva of *Eurytoma* sp. eventually would have destroyed the larva of *E. trisulcus* or *vice versa.*

Though the detailed life-history of *E. trisulcus* has not been studied, the presence of a long ovipositor on this and closely allied species found in galls, indicates that oviposition frequently takes place in galls in which the occupants of the cells are well protected beneath a deep layer of plant tissue. Moreover, the protracted and irregular emergence of the adults of *E. trisulcus* indicates an absence of any close correlation with the primary gall formers in the various instances, such as the writer has shown to exist in *Epimegastigmus brevivalvus* and *Megastigmus acaciae* (Noble, 1938*a*, 1939*b*). *E. trisulcus* does, however, destroy the larvae of the primary gall-forming species, and when laying in mature galls it is very doubtful if its larva feeds at all phytophagically.

Eurytoma spp.

As was found to be the case in flower bud galls on various species of *Acacia* caused by *T. acaciae-longifoliae*, three species of *Eurytoma* were present in the galls on *Acacia implexa* and all resulted in the destruction of the primary gall former. There was considerable competition amongst the various species and also amongst individuals of the same species of *Eurytoma*. This is indicated in Table 3, where, although only one individual could survive, up to nine eggs of various species might be laid in a single gall cell. Of the three species of *Eurytoma* present, *E. gahani* Noble and *Eurytoma* sp. B. occurred most commonly, emerging from the galls in much larger numbers than did the primary gall former *T. maideni*. The egg of a third species of *Eurytoma* was also occasionally observed in the gall cells. This egg, which was dark brown, consisted of an oval body and a short and a long pedicel (Fig. 4E) and had the surface of the body covered with short, sharp-pointed black spines, and was similar to one described by the writer (Noble, 1940) found occasionally in galls on acacias caused by *T. acaciae-longifoliae*.

TABLE 3.

Results of Examinations of Single Cells from Galls on Acacia implexa *caused by* Trichilogaster maideni.

Date of dissection.	Stages and condition of *T. maideni* larvae present.	*Eurytoma* sp. B. Eggs.	*Eurytoma* sp. B. Larvae.	*Eurytoma* sp. eggs.	Total eggs and larvae present in cell.
14.i.1937 ..	Third stage—alive	2	—	1	6*
23.i.1937	Third stage—dead	—	1 first.	1	3
	Third stage—dead.	—	1 first.	5	7
	Fourth stage—dead	1	1 third.	—	3
	Fifth stage—dead	5	1 second.	—	7
25.i.1937 ..	Third stage—dead	5	1 first.	—	7
26.i.1937	Second stage—dead	7	1 first.	—	9
	Fourth stage—dead	4	2 first (dead). 1 third (alive).	—	8
	Third stage—dead	4	1 first.	—	6
	Fourth stage—dead	4	1 first.	—	6
6.v.1937 ..	Fifth stage—alive.	—	1 first.	—	2

* Two unidentified larvae.

Eurytoma gahani *Noble.*

This species was also found by the writer in association with *Tepperella trilineata* Cameron (see Noble, 1938*b*), and with *Trichilogaster a-longifoliae* (see Noble, 1940), and the detailed life-history in association with *Tepperella trilineata* has already been published by the writer (see Noble, 1939*a*). Its life-cycle is annual. Its egg is laid alongside the egg or larva of *T. maideni*, the two species of larva living phytophagically in a normal association for many months until the larva of *T. maideni* reaches the last stage and is maturing. The larva of *E. gahani* on reaching the fifth stage devours the larva of *T. maideni*, pupates in the gall cell, and eventually emerges as an adult from the gall.

Of 507 gall cells examined in October, 1936, 165 contained normal larvae of both species, while in a further 231 cells the larvae of *T. maideni* had already been devoured; *T. maideni* was present alone in only 94 cells, figures which indicate the dominance of *E. gahani*. The great majority of the larvae of *T. maideni* are devoured during October, though a few are devoured some time before this, and a period of many months may then elapse before *E. gahani* eventually emerges as an adult, and most of this time is spent in the mature larval stage.

Emergence of adults of *E. gahani* commenced on 3rd November, 1936, the same day as the first adult of *T. maideni* emerged, but emergence continued until 6th April, 1937, an emergence period of over five months. By far the greatest numbers emerged during the month of January, and at this time on sunny days large numbers were to be seen either on the wing or ovipositing within the minute new season galls. Adults of *E. gahani* which emerged as late as April, 1937, were quite normal, but in most instances would have to deposit their eggs alongside larvae of *T. maideni* which had reached the third or fourth stage.

Eurytoma sp. B.

This species occurred very abundantly in the galls on *Acacia implexa* and has already been mentioned by the writer, it having been observed in association with *T. a-longifoliae* (Noble, 1940, p. 33). Specimens were forwarded to the late Mr. A. A. Girault, who informed the writer that he was describing the species as new, but a description has not yet been seen.

The Adult.—The adult female is a typical member of the genus *Eurytoma*, being dominantly black, with the abdomen laterally compressed and varying from reddish-brown to black. The abdomen is strongly curved and keeled, being drawn out to a fine, slightly upturned tip. Its length averages 3·33 mm., the maximum being 3·54 mm. and the minimum 3·07 mm.

The Egg.—The ovarian egg (Fig. 4B) consists of a white oval body, a short pointed anterior pedicel and a long posterior pedicel. After deposition (Fig. 4C) the egg becomes dark brown and the shell can be found in the gall cell months after the larva has hatched. The total length of the egg averages 0·998 mm., the anterior pedicel being 0·082 mm. and the posterior pedicel 0·523 mm.; the body of the egg averages 0·394 mm. in length and 0·140 mm. in width. Sometimes the long pedicel becomes somewhat twisted after deposition, but it may more or less retain its original shape, and the size of the body of the newly deposited egg is much the same as that of the egg just prior to deposition.

First Stage Larva.—The first stage larva (Fig. 4A) is more or less translucent and consists of a head and thirteen clearly defined segments. It is more or less straight in outline, and is somewhat dorso-ventrally flattened. The third, fourth and fifth segments are widest, the larva tapering conspicuously to both ends. The head and the first abdominal segment are much more heavily chitinized than the remainder of the larva and are amber. The smallest larva measured was 0·512 mm. in length and 0·17 mm. in width, the width of the head being 0·12 mm.

The head is somewhat triangular in outline, the mouth being situated on a downwardly directed prominence. Dorsally, the head carries a pair of cylindrical short antennae and on the dorsal surface of the head there is one pair of long setae and behind these a shorter pair. On the ventral surface of the head there is also a pair of long setae, and there are two lateral and shorter pairs with a minute pair above the mandibles, making a total of six pairs of setae on the head. The mandibles are amber, sharp pointed, curved and unidentate, the tips overlapping, their length averaging 0·016 mm.

All the body segments bear large numbers of minute short pointed spines. On each segment there is a dorsal pair of long setae. On the first three segments there are two ventral pairs of long setae, and on each of the succeeding segments there is a pair of ventral setae which becomes shorter on the posterior segments. On the first abdominal segment there are two minute semi-circular chitinized structures of unknown function. In newly hatched larvae no tracheal system could be distinguished, but during the first larval stage an open respiratory system develops. Four pairs of spiracles are present, one pair on segments 2, 4, 5 and 6. There are two delicate longitudinal tracheal trunks and a limited number of fine branches.

In general structure, shape and setae distribution, the first stage larva of *Eurytoma* sp. B. is remarkably similar to that of *Eurytoma rosae*, a parasite of *Cynips coraria* (see Parker, 1924).

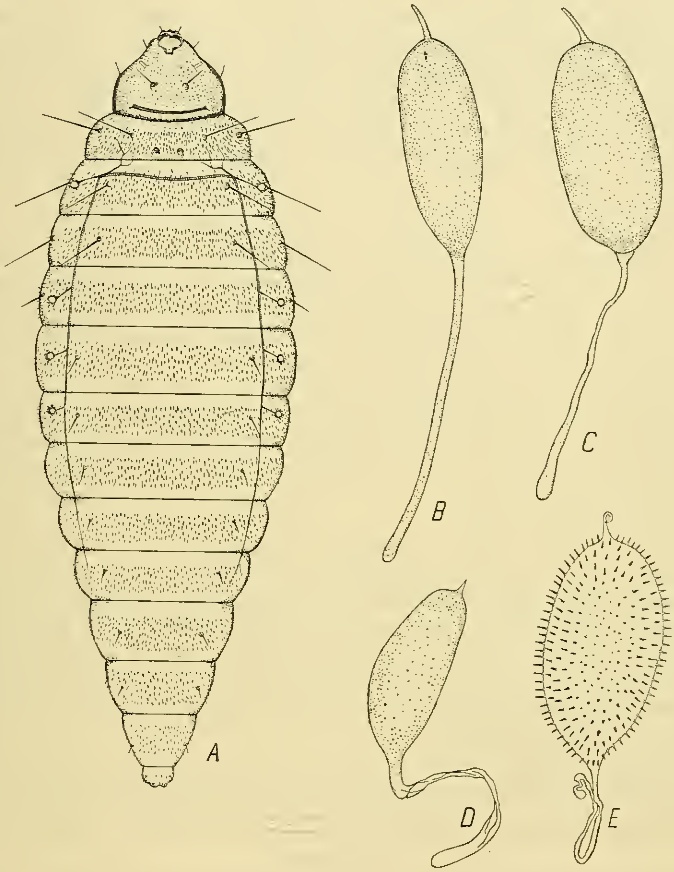

Fig. 4A.—*Eurytoma* sp. B. Ventral view of first stage larva from gall cell on *Acacia implexa* (× 130) ; Fig. 4B.—*Eurytoma* sp. B. Ovarian egg (× 70) ; Fig. 4C.—*Eurytoma* sp. B. Egg shortly after deposition (× 70) ; Fig. 4D.—*Epimegastigmus* (*Megastigmus*) *trisulcus*. Egg dissected from gall cell on *A. implexa* a few hours after deposition (× 70) ; Fig. 4E.—*Eurytoma* sp. Egg found in cell of gall on *A implexa* caused by *Trichilogaster maideni* (× 70).

Oviposition.—*Eurytoma* sp. B. mated readily under laboratory conditions and was observed on a number of occasions ovipositing in the field. The female of *Eurytoma* sp. B. is apparently able to detect the presence of *T. maideni*, and with the ovipositor, penetrates the plant tissues and deposits an egg alongside whatever stage of *T. maideni* happens to be present. In 1936, the first adult of *Eurytoma* sp. B. emerged on 7th November, only four days after the first adult of *T. maideni* emerged, so that at this time the egg of *Eurytoma* sp. B. is deposited alongside the egg of *T. maideni*. Emergence continued until August, 1937, a period of almost ten months, and by the time the last adults emerged *T. maideni* had reached the last larval stage in the new season galls, and the eggs of *Eurytoma* sp. B. are then laid alongside these larvae. The eggs, being dark, stand out conspicuously and often adhere to the integument of the larvae of *T. maideni* when the latter are removed from the galls.

During late 1936, and early 1937, the eggs of *Eurytoma* sp. B. were found in cells with first, second, third and fifth stage larvae of *T. maideni*; the exact stage of development of the host at the time *Eurytoma* sp. B. oviposits appears to be of little significance.

Larval Development.—It is evident that *Eurytoma* sp. B. is a parasitic species, and soon after its characteristic larva hatches it attacks and destroys any other eggs or larvae which are in the cell, including those of the same species, in cases of superparasitism.

These active first stage larvae have frequently been found in cells with the dead remains of host larvae of various stages, and the crushed eggs and first stage larvae of its own species and the eggs of *Eurytoma gahani*. In Table 3 are set out the results of the examination of a number of cells in galls on *Acacia implexa*. It will be seen that the number of original occupants, including eggs and larvae, ranged from two to nine in single cells, six and seven being quite common. It is evident that there is a considerable struggle for existence, as only one occupant of each cell can hope to reach the adult stage.

In dissections in March, 1937, it was not uncommon to find no living occupant in the gall cells, but masses of debris which, examined microscopically, proved to be egg shells and dead larval remains of various species of wasps, the intensity of the competition having resulted in the death of all the occupants. In this struggle, the larvae of *T. maideni* suffer severely, and the great majority which hatch are destroyed by the various species of *Eurytoma* before they mature. This accounts for the very limited emergence of *T. maideni* adults as compared with those of other species, its survival, no doubt, being assisted by its ability to lay eggs in such large numbers.

As the life-cycle is annual and the larva of *Eurytoma* sp. B. is only quite small when its host has been destroyed, the remainder of its larval life must be spent phytophagically. (For an account of somewhat similar behaviour in *Eurytoma studiosa* and *E. auriceps* see Triggerson, 1914.)

Emergence of Adults.—Adults commenced to emerge on 7th November, 1936, and emergence continued until August, 1937, a period of almost nine months after the last adult of *T. maideni* emerged. Galls from which these adults emerged were picked from the trees on 30th October, 1936, and for many months were hard and dry, and could have supplied no food to the insects. Dissections in the intervening period always showed some mature larvae lying in hard dry cells, so it is evident that this species, like *Eurytoma gahani*, can spend very long periods in the mature larval stage in hard dry galls and yet emerge normally.

Females of *Eurytoma* sp. B, in the laboratory, lived longer than any of the other gall-infesting species studied, many being alive and active a month after emergence.

Trichilogaster maideni causing Galling of the Stems of Acacia Maideni.

Introduction.

T. maideni has been found by the writer to cause fleshy elongate, irregular stem galls on *Acacia Maideni* (Pl. viii, D). Two infested trees, only, have been observed by the writer in the Sydney district, but on both trees there were few stems which were ungalled, the entire trees presenting a gnarled and unhealthy appearance. Observations on the development of these galls were made over a period of two years, commencing in 1936.

The morphology of the egg and larval stages was indistinguishable from similar stages of *T. maideni*, causing galls on *Acacia implexa*, but there were minor differences in the adults, and distinct differences in biological behaviour. At various times adults of *T. maideni* bred from galls on *Acacia Maideni* were enclosed with young twigs from *Acacia implexa*. They displayed no interest, though *T. maideni* bred from galls on *A. implexa*, readily oviposited under similar conditions. As suggested earlier, there are apparently two subspecies or varieties of *Trichilogaster maideni* involved.

The emergence period of adults of the two forms is more than a month apart; different hosts are selected; oviposition occurs in somewhat different positions and produces galls of entirely different appearance, and while no males of *T. maideni* were ever observed in galls on *A. implexa*, males of this species emerged quite freely from galls on *Acacia Maideni*.

The Adult.

The Female.—While resembling adults bred from galls on *A. implexa* very closely, they are slightly smaller. Their average length is 2·81 mm., the maximum being 3·13 mm. and the minimum 2·66 mm. The general appearance, and the general pigmentation of the head, thorax, abdomen and legs of the two are much the same, but the ochreous markings on the dorsal surface of the third and fourth segments usually extend further down the sides of the abdomen, and in most specimens there is also a variable ochreous patch on the posterior portion of the dorsal surface of the fifth segment; thus the ochreous patch on the abdomen frequently appears divided into two unequal areas by the dark brown anterior portion of the fifth segment.

The Male.—The average length of the male is 2·15 mm., the maximum being 2·29 mm. and the minimum 1·93 mm. It is much shorter and less robust than the female. The head is black, apart from the eyes, which are dark reddish-brown, and the antennae are brown. The thorax is black and the abdomen varies from dark brown to black, the legs being similar in colour to those of the female.

The Egg and Oviposition.

The egg, which is similar in every way to that laid by *T. maideni* in *Acacia implexa*, is inserted by the females in the young twigs which have developed at the tips of the branches a few weeks earlier. The female after laying an egg moves on a little, and repeats the process, and it is quite common to see a number of females laying in various parts of the same twig, the extensive galls which develop subsequently representing the result of the deposition of many hundreds of eggs by a number of females. As the adults are short lived and emerge mainly in November and December, oviposition mainly occurs during those two months.

The eggs in ten newly emerged females were counted, the average being 397·3, the maximum being 589, and the minimum 262.

Larval Development.

In 1937 periodic dissections of galls were made from 10th May until 26th October, and the various stages of larvae present are set out in Table 4. In May definite, but very small, galls were present, and it will be seen that only second and third stage larvae were dissected. It will be noted that there is a steady development of the larvae during the winter and following spring, coinciding with the gradual increase in size of the galls themselves. Fifth or last stage larvae were first dissected on 9th September, and prepupae were first found on 26th October. On 29th October, several hundred gall cells from this same tree were examined, and while most were occupied by either immature or mature larvae, a few cells contained pupae and several contained adults of *T. maideni*, so that there is considerable overlapping of the various stages.

TABLE 4.
Results of Dissection of Galls on Acacia Maideni *showing Stages of* Trichilogaster maideni *Present.*

Date of dissection.	No. of cells examined.	Larvae.					Prepupae.
		Stage I.	Stage II.	Stage III.	Stage IV.	Stage V.	
10.v.1937	27	—	8	19	—	—	—
28.vi.1937	28	—	3	13	12	—	—
9.viii.1937.. ..	30	—	5	23	2	—	—
9.ix.1937	23	—	—	—	2	21	—
5.x.1937	44	—	—	—	7	37	—
26.x.1937	40	—	—	—	—	35	5

First adult of *T. maideni* emerged 6.xi.1937.
Last ,, ,, ,, ,, ,, 28.xii.1937.

The Pupa.

The female pupa is at first white, but becomes pigmented fairly rapidly. The head and the thorax become black, but only the anterior borders of each abdominal segment become black, the remainder being brown, so that the abdomen presents a striped appearance. The average length of the female pupa is 2·46 mm., the maximum being 2·71 mm. and the minimum 2·19 mm. The male pupa remains lighter in colour during the greater part of the pupal period, but it exhibits the banded appearance of the abdomen as does the female. Its length averages 1·90 mm., the maximum being 2·08 mm. and the minimum 1·77 mm.

Emergence of Adults.

In 1936, emergence began in the latter half of November, and adults emerged in large numbers during the first half of December, and limited numbers emerged until towards the close of that month. In 1937, the first adult of *T. maideni* emerged on 6th November, and emergence continued until 28th December, an emergence period of almost two months.

Total Life-Cycle.

The life-cycle is annual, and, as with other acacia gall wasps, the incubation period and the pupal period are relatively short, the larval period being by far the most extensive stage of the life-cycle.

OBSERVATIONS ON THE DEVELOPMENT OF THE GALLS.

Egg-laying in the young acacia twigs takes place mainly in November and December, but it is not until some months later that there is any definite external evidence of galling.

Examination of the tree on 11th April, 1937, showed some of the twigs were swollen and uneven on the surface, this being the first indication of gall formation (Pl. viii, B). Moreover, some twigs in which galls subsequently developed appeared to be quite normal at this time.

The progress of gall development is a steady one extending through the late autumn, the winter and the spring. By 10th May, 1937, while a few of the galls were just about half grown, others were just showing a slight roughening of the surface. Second and third stage larvae of *T. maideni* were present at this time. The surface of all of the galls at this time was fairly regular. By 28th July, 1937, the smallest galls were about half their full size. At this time the galls were soft and fleshy, and could be cut with ease.

Growth appears to accelerate in the early spring and inspection on 9th September showed that the more advanced galls were almost their full size. Such galls were found to contain larvae of the last stage, though they were not mature. By the 5th October, 1937, most of the galls had reached their full size, and of 44 larvae dissected on that date 37 were in the last stage. On 26th October, 1937, all galls were full size, and none could be found which did not contain last stage larvae of *T. maideni.*

As development progresses, the galls become more irregular in outline, and at maturity consist of a number of rounded swellings which stand out above the general surface of the gall (Pl. viii, D.). The outer surfaces of the galls are bright olive green, and for the most part this general colour is maintained throughout gall development. In some instances there is a cracking or scaling of portion of the gall surface, which gives it a brownish coloration. The individual lengths of galled twig vary from less than an inch up to one foot, and while usually the galls incorporate the whole of the circumference of the twig, occasionally small galls containing a limited number of occupants develop on one side of the stem only. Though the percentage of moisture in the galled tissue does decrease as the galls mature, they never become hard and woody as do those on *Acacia implexa.*

Soon after adults emerge from the galls, the latter commence to turn black, and in most instances the twig dies, though the previous season's galls may persist in a dead condition on the trees for at least twelve months. Sometimes the twig and foliage beyond the galled stem have remained alive for twelve months after the emergence of the adults, and quantities of gum may exude from the emergence holes.

Several hundred adults may emerge from a single elongate gall, the individual cells in the gall being very close to one another, and not regularly arranged. In crowded galls some of the occupants are sometimes deep down and completely overlain by others, and though as many as twelve males have been found in adjoining gall cells, the two sexes appear to be scattered irregularly through the galls.

The plant tissues at first fit closely around the larvae, and while with larval development a small space does develop between the larva and the wall of the cell, a large cell is never formed, the gall cell or chamber being only slightly larger than the larva at maturity.

INSECTS ASSOCIATED WITH TRICHILOGASTER MAIDENI IN GALLS ON ACACIA MAIDENI.

No lepidopterous larvae were found in these galls, but, as well as the Anthribid *Doticus pestilens*, seven species of Chalcidoids emerged from the galls, in addition to the primary gall former, *T. maideni*. These included *Eurytoma gahani*, *Eurytoma* sp. B., *Megastigmus trisulcus* and *Coelocyba nigrocincta*; the two first mentioned species have been discussed earlier.

Coelocyba nigrocincta *Ashmead.*

Numbers of adults of this species emerged from the galls on *A. Maideni*. The species was first described from agromyzid galls on *Eucalyptus corymbosa*, and was bred by the writer from galls on *Acacia decurrens* caused by *Tepperella trilineata*, from galls on *Acacia implexa* caused by *Trichilogaster maideni*, and occasionally from galls on *Acacia floribunda* caused by *Trichilogaster acaciae-longifoliae*.

Examination showed that adults and pupae of *C. nigrocincta* were to be found in separate cells in the galls, scattered through the other gall cells occupied by various stages of the primary gall formers. In a number of instances the pupae of *C. nigrocincta* were removed from cells and all the debris was mounted on slides and examined, and on several occasions the mandibles of mature larvae of *Trichilogaster maideni* were also found in the cells.

The detailed life-history of this species has not been studied, but an egg (Fig. 5E) was dissected from a globular flower head on *Acacia decurrens*, in which the eggs of *Tepperella trilineata* had already been deposited. It is evident that *C. nigrocincta* causes the death of the primary gall former, but that the latter is at least able to reach the last larval stage before destruction.

On the various species of *Acacia* under discussion, where unilocular galls were found to contain only pupae or adults of *C. nigrocincta*, these were similar in appearance to unilocular galls in which the primary gall former only was present.

The Adult.—This species was described by Ashmead (1900), the genus *Coelocyba* being also then established. He placed it in the family Pteromalidae. Girault (1916, p. 222) considered it incorrectly placed and removed the species to the family Perilampidae.

The writer found that there was considerable variation in the size of the adult, the average length of the female being 2·74 mm., the maximum being 3·18 mm., and the minimum 2·45 mm. The male is very much smaller than the female, the average length being 1·83 mm., the maximum being 2·03 mm., and the minimum 1·46 mm. Occasionally very minute adults emerged from galls on *Acacia Maideni*, one such female measuring 1·46 mm., and one male 0·99 mm. The antenna (Fig. 5B), mandible (Fig. 5D) and stigmal knob (Fig. 5C) of the female, and the antenna (Fig. 5A) of the male are figured.

Both sexes are remarkably active, and when confined in tubes or jars in the laboratory run around rapidly.

The Egg.—The ovarian egg (Fig. 5F) differs little in shape from the egg after deposition (Fig. 5E). Both are smooth-surfaced, elongate and oval, slightly arched with rounded ends. The average length is 0·31 mm., and the average width 0·065 mm.

Emergence of Adults.—Emergence of adults is rather irregular. Galls were collected from *A. Maideni* on 1st November, 1937, and a number of *C. nigrocincta* emerged on that day. The first adults of *T. maideni* did not emerge until 6th November, and adults of *C. nigrocincta* continued to emerge periodically throughout, and after the emergence period of the primary gall former.

Parasitic Nematodes associated with C. nigrocincta.—In 1936 and also in 1937 in dissecting adults of *C. nigrocincta* from galls on *Acacia decurrens*, *A. Maideni* and *A. implexa*, parasitic nematodes were to be found free in the abdomens of both sexes (Fig. 5J). The parent nematodes at this time were capable of only very slight movement, but, within, young nematodes could be seen twisting and turning and at times temporarily thus changing the outline of the parent. When the integument of the parent nematode was torn open, numbers of crescent-shaped living young floated out (Fig. 5G).

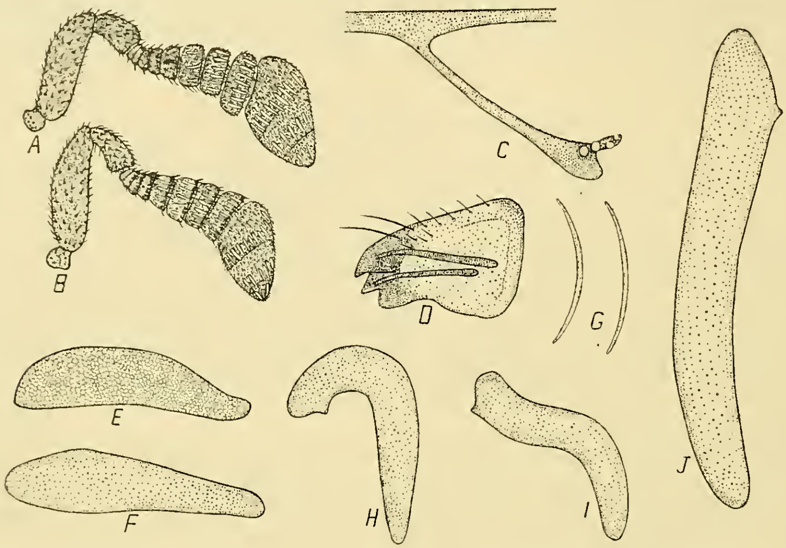

Fig. 5.—*Coelocyba nigrocincta.* A, Antenna of male (× 65); B, Antenna of female (× 65); C, Stigmal knob of female (× 122); D, Mandible of female (× 122); E, Egg after deposition (× 122); F, Ovarian egg (× 122); G, Young nematodes dissected from abdomen of adult of *C. nigrocincta* (× 42); H, I, Immature nematodes dissected from pupa of *C. nigrocincta* (× 42); J, Mature nematode containing living young dissected from adult of *C. nigrocincta* (× 42).

The mature nematode varies from translucent to light green, and was always found in the abdomen of the wasp.

Nematodes in each wasp ranged from one to twenty, the average number being 4·9. The average length of the gravid nematodes was 1·29 mm., the average width being 0·20 mm. The largest gravid nematode measured 1·6 mm. in length and 0·24 mm. in width, while the smallest nematode measured 0·90 mm. in length and 0·19 mm. in width.

One gravid nematode was found to contain 75 young. The size of the young nematodes found floating freely in the host haemocoele varied somewhat, the average length being 0·39 mm. and the width at the widest point 0·013 mm.

In 1936, of 72 females of *C. nigrocincta* examined, 28 contained nematodes, while only 3 of the 14 males examined were nematode infested. In 1937, only 6 out of a total of 50 females contained nematodes and 9 out of 38 males were nematode infested.

In both 1936 and 1937, pupae of *C. nigrocincta* were dissected from galls and were found to contain nematodes which were not quite fully developed. The average length of three was 0·74 mm. and the average width 0·12 mm. (Fig. 5H, I); none of these contained living young, but usually in adult wasps young nematodes were present within their parents.

Both males and females of *C. nigrocincta* infested with nematodes were quite active and just as large as those which were uninfested, so that the presence of the nematodes could only be detected by dissection. Internally, infested individuals were found to be in an unthrifty condition. The alimentary tract was intact, but there was a notable absence of fat-body, and in the case of female wasps the ovaries were distinctly reduced, and in some instances almost wanting. The general condition of all the internal organs was definitely unhealthy.

AUSTRALIAN CHALCIDOID GALLS.

Detailed life-history studies of a number of species of Australian gall-forming Chalcidoidea have now been published (Noble, 1936, 1938*b*, 1940). General observations on a number of other species of gall formers have also been made, and all have certain features in common.

In the citrus gall wasp, *Eurytoma fellis* (Noble, 1936), the ovarian egg consists of an oval body and a short anterior, and a very long posterior pedicel. The ovarian egg of *Tepperella trilineata* (Noble, 1938*b*), of all species of *Trichilogaster* studied, and of several other species of gall-forming wasps under observation, consists of an oval body and an elongate pedicel, which has become so enlarged posteriorly, that the egg now appears as a bilobed structure joined by a narrow connecting tube. This greatly enlarged pedicel is apparently a device to facilitate the passage of the egg down the narrow ovipositor. The plant tissues within which the eggs are deposited are always delicate, and it is important that the wasp in inserting the egg should cause a minimum amount of injury to the host plant. Following oviposition in all cases, the protoplasmic contents pass into the body of the egg, the vitelline membrane soon surrounding the developing embryo, cutting it off from the now flaccid pedicels.

In their oviposition behaviour the various wasps studied also behave somewhat similarly. The eggs are invariably laid in some recently formed plant tissues, either leaves, stems or flower buds, which are still very soft and young, and which under ordinary circumstances in the ensuing months, even in the absence of insect attack, would have undergone great development and increased considerably in size. *Eurytoma fellis* and *Trichilogaster maideni* select for oviposition recently developed stems, but *Trichilogaster acaciae-longifoliae* (Noble, 1940) and *Tepperella trilineata* select for oviposition, minute flower buds at a very early stage of development.

The life-cycle of all primary gall-forming wasps so far studied in Australia is annual, the adult wasps emerging from the galls each year during the late winter, spring or early summer. In all cases the incubation periods and pupal periods are rather limited, the larval period representing by far the longest period of the life-cycle and lasting nine months or more. The length of adult life in all species is comparatively short, the female wasps always being ready to lay immediately after they emerge from the galls; by far the greatest oviposition occurs during the first twenty-four hours after emergence.

Slight abnormalities in the plant tissues usually manifest themselves within a few months of oviposition, but while gall development in each case only occurs once in each twelve months, there is considerable variation in the length of the period which elapses after oviposition, before the first signs of galling become evident. In citrus stem galls caused by *Eurytoma fellis* first signs of twig unevenness appear soon after the larvae have hatched, and external gall development is complete when the larvae are still in the first stage. In *Trichilogaster maideni*, which also produces twig swellings, the galled stems increase in a regular manner throughout the entire larval period, and reach their full size in the following spring at the time the larvae reach maturity. With *Tepperella trilineata* and *Trichilogaster a-longifoliae*, which oviposit in the minute flower buds, no definite evidence of galling is present until some months after the larvae have hatched. This is especially true of *T. a-longifoliae* where, following oviposition in *Acacia floribunda* and *A. longifolia*, only extremely minute galls are to be seen six months later, the typical large green fleshy galls being present on the trees for only a few months of the year.

In the earlier stages of gall development the plant tissues are in contact with the various species of larvae and at this time these have either a closed or very limited open respiratory system. With the progress of larval growth, a limited space develops between the inner wall of the nutritive layer and the integument of the larva, this being accompanied by a further development of the respiratory system.

At maturity the larva is to be found in a cell, which is always somewhat larger than the larva itself and, although enclosed in the gall, the larva then possesses nine pairs of open spiracles and a well developed respiratory system, which appears to be just as complete as that possessed by an external feeding larva of this group.

Types of Gall.

It is evident that the galls caused by Australian Chalcidoids may be divided into two general groups. In the first, oviposition and subsequent larval development results in generalized twig swellings, in which, even at maturity, the original botanical units can still be distinguished, though they are somewhat abnormal. Galls of this type are the twig swellings on various species of citrus caused by *Eurytoma fellis*, and twig swellings on *Acacia Maideni* caused by *Trichilogaster maideni*. Similar twig swellings caused by another species of *Eurytoma* have also been observed by the writer on various species of *Eucalyptus* in the Sydney district. The effect of such twig galling varies somewhat with the different species of trees and the insects, as well as the age and the portions of the trees attacked, but under all conditions the general effect on the growth and further development of the entire tree, or infested limbs, is rather severe. Twig swellings of this type, though large, may persist in a living condition with the various conducting tissues functioning for some years. In an experiment in November, 1931, the main stem of a seedling lemon tree was infested with the gall former, *E. fellis*. The seedling was then only six months old. Typical galls developed in the following autumn and winter, and each year since that time, up to 1939, the tree has put out new growth above the galls of the previous year, this new growth each spring being infested by the newly emerged wasps. Plant food to reach the upper leaves must be carried through several feet of galled tissues. This tree, though still alive, is extremely stunted and abnormal. Where galls have been caused by *Trichilogaster maideni* on *Acacia Maideni*, it is not uncommon for the entire tissues above the galled stem to die within a few months of emergence of the adults, though occasionally such galled stems have been observed to function for at least twelve months after the emergence of the wasps. The galling of a limited number of lateral stems has only a comparatively slight effect on the general health of the tree, as abundant new growth develops from the ungalled twigs, but after years of infestation, almost every new twig on the tree is galled each spring, and the entire tree eventually assumes an extremely unhealthy and unsightly appearance. In young trees, if heavy oviposition and galling occur in the main stem, the tree never develops satisfactorily if the galls are left, and if the galled tissue is cut away, the shape of the tree is ruined.

The second general group of galls is that in which oviposition and subsequent larval development result in the production of outgrowths or proliferations of various parts of the host. Such galls stand out conspicuously, and, though at times very large, they are often only connected to the tree by very narrow attachments. Examples of such galls are those formed in the flower buds of *Acacia decurrens* by *Tepperella trilineata*, the galled flower buds of various species of *Acacia* caused by *Trichilogaster a-longifoliae* and small globular galls caused by Chalcids on the leaves of various species of native shrubs. In such galls it is often extremely difficult, once gall formation has progressed very far, to trace the changes in the original botanical units. After the wasps emerge from such galls the latter shrivel within a few weeks and die, and eventually drop from the trees, though it may be a year or more before all of the previous year's galls ultimately disappear. In these galls it appears that the host plant succeeds in cutting off and isolating the invading insects, so that in their final effect upon the tree, they are far less injurious than the wasps which cause twig swellings.

Recently the writer has studied a Chalcidoid which oviposits in the young leaf buds of Turpentine (*Syncarpia laurifolia*); subsequent larval activity eventually results in the development of large numbers of minute unilocular galls on the foliage, as many as 142 galls having been counted on a single leaf. As the leaves eventually fall and are replaced by others, such insects have little ultimate effect on the vitality of the tree, unless almost all the leaves are so heavily infested that they cannot function normally. However, this seldom appears to occur.

It is known also that in Australia some species of Chalcidoids infest the seed capsules of various native plants causing some abortion of the tissues and a loss of seed, but no detailed observations on these have yet been made.

The Experimental Production of Galls.

For the detailed study of the life-history of a gall wasp, undoubtedly the ideal method is to produce numbers of galls experimentally so that these, with a known history, can be dissected from time to time and the stages of the insect present noted. This, however, may prove either extremely difficult or even impossible. This has been confirmed by Kinsey (1920, p. 323), who has worked extensively with American cynipid gall wasps. He considered, moreover, that trees on which galls are to be produced must be in a very vigorous condition.

When working with the citrus gall wasp, *Eurytoma fellis*, the writer found little difficulty in producing galls experimentally in the insectary, and for several years large numbers of potted citrus seedlings were experimentally galled and were infested both with *E. fellis* and its parasite, *Epimegastigmus brevivalvus*, and the potted trees used for this work were certainly growing vigorously at the time of infestation. Similarly, little difficulty was experienced in inducing the experimental production of galls on *Acacia longifolia* growing in pots, by merely enclosing newly emerged females of *T. a-longifoliae* with these trees in large cellophane sleeves.

However, with *Tepperella trilineata*, which causes galls on the flower buds of *Acacia decurrens* var. *pauciglandulosa*, the writer met with no success. For four consecutive years, in the spring, many hundreds of adults were enclosed in cellophane sleeves of various sizes with twigs and large branches on particularly vigorous young host trees. In addition, branches bearing mature galls were hung in these trees during the early emergence period of *T. trilineata*, but though extensive oviposition was observed on many occasions, and some galls commenced to develop, not a single mature gall was secured. An inspection of a number of host trees of the same variety in various localities failed to show any vigorous young trees carrying galls caused by *T. trilineata*. Such galls were only found on trees which had been growing for many years, and the only tree observed by the writer which was very heavily galled was one which was in a very unthrifty condition, borer infested, and on which a number of the limbs were already dead.

It would appear that while, in many instances, a certain vigour in the host plant is an essential pre-requisite to successful gall formation, in others, a vigorously growing host is apparently not essential.

The Causes of Gall Development.

While it is clear that the hypertrophy which results in the development of galls is in some way attributable to the insect, the exact nature of the stimulus which results in gall development has never been discovered. The findings of workers with Cynipids can in certain respects be substantiated by observations of the writer with the Australian chalcidoid gall wasps. The insertion of the ovipositor or any fluid which might be injected together with the egg, or the presence of the egg itself, in all species studied by the writer, is in no way directly connected with gall formation.

It has been suggested that the secretion of some product or products by the larva may cause the plant tissues to hypertrophy. Triggerson (1914) considered that in the case of the Cynipid, *Dryophanta erinacei*, the development of the gall is due to the excretion of a fluid from the malpighian vessels in the larva.

The writer (1936) sectioned, at various stages of development, galls on citrus caused by *E. fellis*. These showed that the egg is deposited between the xylem and phloem in contact with the cambium layers, and the young larva commences development in this position. In this species, as well as in all the others studied, there was no evidence of gall formation until some time, at least, after the larva had hatched, and in every instance gall formation was complete either during larval development or at latest by the time the larvae reached maturity. Thus it is evident that the formation of galls has in some way been due to the presence of the gall wasp larva, and the effect of the latter on the meristematic tissues. In experimental trees in which *E. fellis* had oviposited, occasionally, galls were observed to partly develop, and then hypertrophy ceased, and dissection showed that all the gall wasp larvae were dead. This suggests that the continued activity of the wasp larva is essential for the completion of gall development.

It would appear that whatever the stimulus, it must be continued throughout larval life, or at least to a stage in larval development at which the galls reach their full size.

Sometimes the larvae of *T. a-longifoliae* are killed by the larvae of a species of *Eurytoma* at an early stage in gall development and in plurilocular galls, that portion of the gall nearest the cell in which the host larva has been destroyed, and in unilocular galls, the entire gall, ceases to increase in size, though the larva of *Eurytoma* may continue to occupy the gall cell for many months. This suggests that whatever the stimulus, it must be specific to the larva of the particular gall wasp concerned and the suggestion that some larval glandular secretion is responsible for gall formation appears to be a definite probability.

The Effect of Parasitism on Gall Formation.

It has been stated by Froggatt (1892) that the activities of parasites in the galls result in the formation of masses of tissue which have not the shape of normal galls produced by the host gall wasp alone. From the writer's observations, this is only true when parasitism results in the death of the gall wasp larva at an early stage in development and when the galls are only partly grown. If the parasite does not cause the death of the host larva before the latter is maturing, the development of galls is in every way quite normal.

Mature galls on citrus in which a very high percentage of the cells contained larvae of the gall former *E. fellis*, within which there were larvae of *Epimegastigmus brevivalvus*, could not be distinguished from galls in which the host larvae were present alone, but this parasite only destroys maturing host larvae.

Associated with the larvae of *Tepperella trilineata* which cause galls on *Acacia decurrens* was an internal parasite, *Megastigmus acaciae* (Noble, 1939*b*), and also *Eurytoma gahani* (Noble, 1939*a*). The larvae of both of these wasps destroyed the host larvae only when the latter were approaching maturity, and mature unilocular galls containing either species of these parasites were similar in every respect to such galls occupied by the host alone.

The larvae of a species of *Eurytoma* destroyed the larvae of *Trichilogaster a-longifoliae* and *T. maideni* at an early stage in gall development, and where numbers of these parasitic larvae were present in plurilocular galls, completely misshapen and abnormal galls resulted, while mature unilocular galls, though spherical, were hard and woody and only a small fraction of the size of normal unilocular galls occupied by host larvae alone.

Phytophagy and Parasitism in a single species of gall inhabitant.

Gahan (1922) published a list of world species of Chalcidoidea recorded as being phytophagous, and pointed out that such habits in this group were at one time strenuously disputed. Of the phytophagous Chalcidoids listed by Gahan a comparatively limited number produce galls. The Cynipoidea are the dominant gall formers in other countries, but in Australia their place appears to have been taken by an extensive chalcidoid gall-forming fauna, and it is clear that in time there will be large numbers of Australian Chalcidoids to be added to Gahan's world list.

Gahan (1922) in discussing the development of phytophagy in the Chalcidoidea instances, as a point of confirmation of its recent development, the fact that several authors had asserted that certain species of Eurytomidae are parasitic in their early stages and finish their development as plant-feeders (cf. Nielsen, 1906; Rimsky-Korsakov, 1914; Triggerson, 1914; Phillips, 1917, 1927). Published records of such behaviour are still limited and appear to have been confined to the genus *Eurytoma*.

Investigations of the writer have shown that individual species which feed both phytophagically and parasitically occur in Australia, and the life-histories of two such species have been studied in some detail; both of these species belong to the genus *Eurytoma*, viz., *Eurytoma gahani* Noble and *Eurytoma* sp. B. The latter species deposits its eggs alongside the larvae of various species of *Trichilogaster* in galls on *Acacia* spp., and the larva of *Eurytoma* sp. B., on hatching, destroys the host larva and then completes its development phytophagically. *Eurytoma gahani* lays its eggs alongside the eggs or larvae of *Tepperella trilineata* and various species of *Trichilogaster* in galls on *Acacia* spp.; the two species live together in the one cell normally and phytophagically, until the host larva is maturing. At this time the larva of *E. gahani* destroys the host larva and, feeding on its contents, reaches maturity. This appears to be the first record of such behaviour in the Chalcidoidea (see Noble, 1939*a*).

Apart from these two species, the writer has observed five others in which the evidence suggests that these, too, are phytophagous during their early larval period, but later become parasitic or predatory and destroy the host larva. Pupae of two of these, an unidentified species of *Eurytoma* and *Megastigmus* sp. B., have been found in galls on *Acacia longifolia* with the pupal remains of the gall former, *Trichilogaster a-longifoliae*. The writer (Noble, 1940, p. 35) has already pointed out that these host pupae though dead are sometimes almost entire, but are also sometimes entirely devoured. While this indicates some variation in the behaviour of these larvae, it is quite evident that, in some instances, they could not possibly have obtained sufficient nutriment from the host pupa, as *Megastigmus* sp. B. is actually a larger species than its temporary host. As immature *Megastigmus* larvae were several times found in cells with normal host pupae, it is evident that in the earlier part of their life they must have fed phytophagically.

Gahan (1922) concluded that partial phytophagy was probably first forced upon the parasite by the premature exhaustion of the natural food supply, due to attacking a host which was insufficient in itself to furnish food to complete development. It will be noted that in several of the species mentioned above this position is actually reversed, these feeding in the earlier part of their larval life phytophagically and later behaving as parasites. The point arises as to whether, in such species, the parasitic behaviour is one which will eventually give way to complete phytophagy, while it may even be possible that such species may, according to Gahan's theory, have become phytophagous, and that this brief period as a parasite may be recently acquired. It has already been suggested by the writer in regard to *Eurytoma gahani* (1939*a*) that this parasitic habit may arise, not owing to a shortage of parasitic food, but, on the contrary, due to an insufficient supply of plant food, owing to the fact that at the time the host larva in these galls is maturing, a hard woody protective layer surrounds it, and even host larvae alone consume the whole of the nutritive layer prior to pupation.

It is evident that in the genus *Eurytoma* and also the genus *Megastigmus* there exist many species which exhibit a high degree of plasticity, and in view of this the study of species occurring in these groups, particularly in Australian galls, will yield valuable data regarding the evolutionary trends in the Chalcidoidea.

SUMMARY.

The life-history of *Trichilogaster maideni*, a wasp causing galling of the petioles of the phyllodes of *Acacia implexa* and the stems of *Acacia Maideni*, is described. In their biology and host relationships the forms of *Trichilogaster maideni* on *A. Maideni* and *A. implexa* exhibit marked differences. The life-cycle in both cases is annual. The incubation and pupal periods are comparatively limited, the larval period occupying nine to ten months. Adult wasps emerge from galls on *Acacia implexa* during October and November, and from *A. Maideni* from the middle of November throughout December, there being some variation from year to year. No males of *T. maideni* were found in galls on *Acacia implexa*, but they were quite common in galls on *A. Maideni*. The egg and the five larval stages are described. Oviposition commences on the day of emergence, eggs being inserted in the petioles of recently formed phyllodes and young stems.

On *A. implexa*, minute galls are present by the end of January and these increase in size during the following winter and early spring, being their full size at the time the larvae reach maturity. On *A. Maideni*, definite galls are not present until late in the summer, and there is steady growth through the following winter and spring, galls being their full size at the end of October.

Lepidopterous larvae were commonly found mining the galls on *A. implexa*, and the Anthribid, *Doticus pestilens*, emerged from galls on both species of *Acacia*. Eleven other species of Hymenoptera were bred from galls on *A. implexa*, of which eight were Chalcidoids, while in addition to *T. maideni*, seven species of Chalcidoids were bred from galls on *A. Maideni*. Biological notes on some of these species are included.

A number of pupae and adults of both sexes of a Perilampid, *Coelocyba nigrocincta*, which emerged from galls on *A. Maideni*, were found to contain parasitic viviparous nematodes.

The various types of gall caused by Australian Chalcidoids, and experimental gall production, are discussed. Evidence in regard to gall formation indicates that the stimulus is associated only with the larva, and is possibly a secretion. The effect of parasitism on gall development is discussed.

Previous records of the larva of a species being both phytophagous and parasitic are limited, but the writer has observed in Australian galls a number of species of *Megastigmus* and *Eurytoma* which exhibit this behaviour.

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EXPLANATION OF PLATE VIII.

Stages in the development of galls on *Acacia implexa* and *A. Maideni* caused by *Trichilogaster maideni*.

A.—Partly developed galls at the junctions of phyllodes and stems on *Acacia implexa*. Photographed 5.v.1937.

B.—Partly developed galls on the stems of *Acacia Maideni*. Photographed 11.iv.1937.

C.—Mature galls on *Acacia implexa*. Photographed 1.x.1936.

D.—Mature galls on *Acacia Maideni*. Photographed 11.xii.1936. Note occasional emergence holes.

N.B.—The tips of the phyllodes have been cut off.